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Territoriality and Use of Space of the Guacamayo Plump Toad (*Osornophryne guacamayo*) at Guacamayo Mountain Range, Napo Province, Ecuador.

Proyecto de investigación

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UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ COLEGIO DE CIENCIAS BIOLÓGICAS Y AMBIENTALES

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RESUMEN

Osornophryne guacamayo es una especie de sapo bufónido que habita en el bosque montano oriental de Ecuador. Se han realizado investigaciones sobre su taxonomía, pero hay poca información sobre su ecología. El siguiente trabajo, desarrollado en la Cordillera de Los Guacamayos, provincia de Napo, estudia cómo machos y hembras de esta especie utilizan su hábitat. Para esto se utilizaron herramientas SIG y el mapeo KDE 3D de rangos habitables, junto con técnicas de bootstrap para compensar la falta de datos. Se encontró que los machos muestran un arreglo agrupado y las hembras muestran un arreglo disperso. Las gráficas 3D generadas no muestran ninguna diferencia entre ellas, además de superposiciones inexistentes. Los hallazgos apoyan un sistema reproductivo de lek, en donde los machos son altamente territoriales.

Palabras clave: Osornophryne guacamayo, tridimensional, rango habitable, Bufonidae, KDE.

ABSTRACT

Osornophryne guacamayo is a species of bufonid toad that lives in the eastern montane forest of Ecuador. Research has been done regarding its taxonomy, but there is few information about its ecology. The following work, conducted at Guacamayos Mountain Range, Napo province, studied how males and female individuals use their habitat. Home ranges were generated using GIS tools and KDE 3D mapping, along with bootstrap techniques to compensate lack of data. Males show a clustered arrangement and females show a dispersed arrangement. 9 3D plots were computed and show no difference between them, in addition to nonexistent overlapping. These findings support a lek reproductive system and territorial behavior in males.

Key words: Osornophryne guacamayo, three-dimensional, home range, Bufonidae, KDE.

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INTRODUCTION

Osornophryne guacamayo is one of the 11 species that form the genus Osornophryne of the family Bufonidae. (Páez-Moscoso, Guayasamin, 2012, Páez-Moscoso, Guayasamin, Yánez-Muñoz, 2011). This genus is endemic from the paramo and montane forest ecosystems of Colombia and Ecuador (Páez-Moscoso, Guayasamin, Yánez-Muñoz, 2011). Specifically, O. guacamayo has been reported in different localities from the eastern slope of Ecuadorian Andes, as well as a single locality in Colombia, corresponding to the Putumayo region. (Páez-Moscoso, Guayasamin, Yánez-Muñoz, 2011, Mueses-Cisneros, 2003). All these localities correspond to the Eastern Montane Forest, ranging from 1300 meters to 3600 meters in altitude. (Ron, Guayasamin, Menéndez-Guerrero, 2011). O. guacamayo is characterized by having a black-brown dorsal coloration with yellowish lines, in addition of numerous tubercles along all the body. (Hoogmoed, 1987; Fig. 1). The species shows a strong sexual dimorphism in which the female is much larger than the male. (Gluesenkamp, Acosta, 2001). Other sexually dimorphic trait is the venter coloration: in males the venter shows a blackish coloration with yellowish pustules, in females the venter is bright yellow with black spots. (Glusenkamp, Acosta, 2001). As most anurans, O. guacamayo is most active at night, however, there have been reports of specimens collected during daytime. (Guayasamin, Funk, 2009, Gluesenkamp, Acosta, 2001, Gluesenkamp, 1995).

Data concerning the ecology and natural history of this species is limited, a situation that is shared between all members of the genus. Notes by Gluesenkamp (1995) and Mueses-Cisneros (2003) show that *O. guacamayo* was mostly found at 0.5-1.0 meters from the ground on large leaves, with sightings on bromeliads, trunks and exposed leaves. Thus, suggesting an arboreal way of life. The most complete work in this matter is the one provided by Gluesenkamp and Acosta (2001). This work details that perch behavior is not different between sexes and age classes. Nonetheless, most of the individuals were found on short leaves. (Gluesenkamp, Acosta, 2001). In addition, inguinal amplexus was reported, as well as a characterization of the call of a single male. (Gluesenkamp, Acosta, 2001). *O. guacamayo* is inferred to be direct developer, because of sightings of clutches at ground level away from water sites, and reports of terrestrial hatchlings. (Guayasamin, Funk, 2009, Gluesenkamp, Acosta, 2001).

Aspects concerning the territoriality, home range behavior and habitat use by sexes have been reported in diverse species of anurans, but not for *O. guacamayo*. Territoriality has been reported in many species of amphibians (Valenzuela-Sánchez et al, 2014), especially in the family Dendrobatidae. (Pröhl, 2005). Territoriality can be defined as a spatial dominance that assures the holder access to critical resources: food, mates, or breeding sites. (Meuche, Linsenmair, Pröhl, 2012). In the case of anurans, reproduction is the driving cause for the evolution of this behavior. (Valenzuela-Sánchez et al, 2014). The territories are encompassed in the individual's home range, the space in which it obtains all the means to survive. (Neu et al., 2016, Valenzuela-Sánchez et al., 2014, Pröhl, 2005). Territories are necessarily defended and exclusive of the holder, whereas home ranges are not always defended. (Neu et al., 2016). In most species of anurans studied, only males show territorial behavior, with scattered examples of territorial females. (Neu et al., 2016, Meuche, Linsenmair, Pröhl, 2012, Pröhl, 2005).

The research concerning territoriality and home range studies in anurans has been done exclusively in two dimensions, even though most taxa tend to use all space components: depth, altitude and elevation. (Ousterhaut, Burkhart, 2017). Just recently, home range and animal movement research has started to use methods that permit a three-dimensional mapping of how an animal uses its habitat. Kernel methods for home range studies were first proposed by Worton (1989), and subsequently, adapted to study distinct taxa. Three-dimensional adaptations to this methodology have been proposed to map home ranges in fish (Vivancos,

Closs, Tentelier, 2017, Simpfendorfer et al., 2012), birds (Cooper, Sherry, Mara, 2012), megafauna (Tracey et al, 2014), and the closest taxa to our species: salamanders. (Ousterhaut, Burkhart, 2017).

In this study, we took advantage of GIS tools and Kernel methods in the program R to elucidate how male and females of *O. guacamayo* use their habitat and map home ranges of male *O. guacamayo*.



Figure 1. Male Osornophryne guacamayo in its natural habitat. Photo by Claudia Herrera

METHODS

Field work was done at the Jumandy Trail (0.62440° South, 77.84111° West, altitude: 2100 meters) at the Antisana National Park, Napo Province, Ecuador. The ecosystem can be defined as Eastern Montane Forest, characterized by its high humidity. (Sierra, 1999). The trail was located in a steep slope facing south, where the right side was vegetated, and the left side showed a moderately-steep downward cliff.

The study was conducted between the months of January and February 2019, with two field stages: the first of 6 days in January (January 04 through January 09) and the second one of 9 days in February (January 29 through February 06). Mark-recapture methods were used in both stages using nontoxic white body paint in order to reduce handling stress. Indivuduals were actively searched from 19:00h to 00:00h. For the first stage, a 300-meter section of the trail was marked and all individuals of O. guacamayo were measured (snout-vent length), marked with paint, and assigned a GPS waypoint (see below) in order to study the dispersion in males and females. For the second field trip trail markings were placed every 30 meters for 150 meters of transect as references for x-measurements. The temperature, humidity, and weather conditions were recorded at the start and end of each observation period. Toads were marked on the left arm, right arm, left leg, right leg, or back upon the first encounter with each individual. Paint was re-applied on subsequent encounters when necessary. Handling was only used when toads were inaccessible for painting. Coordinates (X, Y, Z) for each toad were obtained with a tape reel. X-coordinates were measured as the horizontal distance between the toad and the start of the trail, Y-coordinates were measured as the horizontal distance from the toad to the middle of the trail, and z-coordinates were measured as the vertical distance from

the toad to the ground at trail level. Reflective ribbons of various colors were placed on vegetation near toad sightings for easier recapture of individuals.

For male and female dispersion analyses we used the tool Nearest Neighbor Analysis, included in the program ArcMap 10.1. We adapted the method of three-dimensional mapping from Cooper, Sherry, and Mara (2014) for *O. guacamayo*. In order to compensate for the lack of movement points, the package "boot" in program R (R Core Team, 2019) was to generate 100 bootstraps in every dimension (X, Y, Z).

RESULTS

During the first part of the study a total of 46 individuals were encountered within the 300-meter transect. 13 of them were female and 33 were male. Of the females counted, two were recaptured at day 4 and one at day 5. (Table 1). On the other hand, of the 33 males, three were recaptured at day 2, eight were recaptured at day 3, 13 recaptured at day 4, and six recaptured at day 5. (Table 2). The temperature ranged between 12 and 13.5 degrees Celsius and the humidity ranged between 75-85%.

During the second field trip a total of 36 individuals were marked in the 150-meter transect. Two of the toads were females and 34 were males. Both females were marked but not recaptured. As for the remaining males, six were recaptured at day 2, eight at day 3, three at day 4, eight at day 5, 11 at day 6, and 13 at day 7. (Table 3). The temperature ranged between 12 and 14 degrees Celsius and the humidity ranged between 76-84%.

The Nearest Neighbor Analysis effectuated in males and females showed different results. (Table 4). Males exhibit a clustered pattern of dispersion (Figure 2), whereas females show a dispersed pattern. (Figure 3).

	Day 2	Day 3	Day 4	Day 5
Ind. 1				
Ind. 2				
Ind. 3				
Ind. 4			Х	
Ind. 5				
Ind. 6				
Ind. 7				Х
Ind. 8			Х	
Ind. 9				
Ind. 10				
Ind. 11				
Ind. 12				
Ind. 13				

Table 1. Recapture rate for female Osornophryne guacamayo in the first field trip

	Day 2	Day 3	Day 4	Day 5
Ind. 1			Х	
Ind. 2		Х	Х	
Ind. 3			Х	
Ind. 4	Х	Х	Х	
Ind. 5				
Ind. 6				
Ind. 7				
Ind. 8		Х	Х	
Ind. 9			Х	Х
Ind. 10				
Ind. 11			Х	
Ind. 12		Х	Х	
Ind. 13				
Ind. 14	Х		Х	
Ind. 15				
Ind. 16				Х
Ind. 17			Х	
Ind. 18				
Ind. 19		Х	Х	
Ind. 20				
Ind. 21	Х			Х
Ind. 22			Х	
Ind. 23		Х		Х
Ind. 24				
Ind. 25			Х	
Ind. 26				
Ind. 27				Х
Ind. 28		Х		
Ind. 29				Х
Ind. 30				
Ind. 31			Х	
Ind. 32				
Ind. 33		Х		

Table 2. Recapture rate for male Osornophryne guacamayo in the first field trip

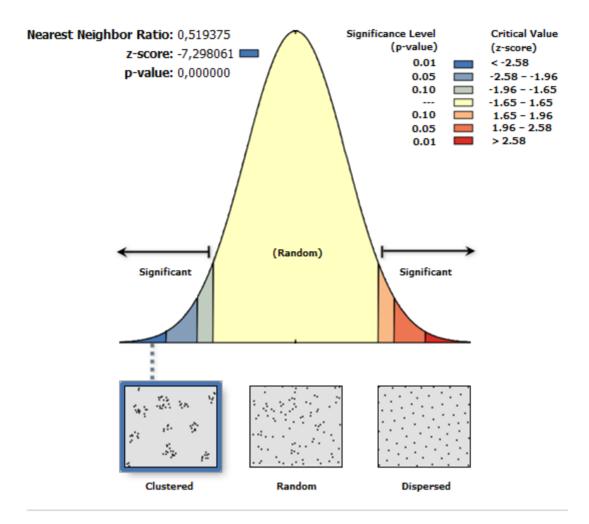
Table 3. Recapture rate for male Osornophryne guacamayo in the second field trip

	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7
Ind. 1	Х					
Ind. 2	Х			Х	Х	Х
Ind. 3	Х					Х
Ind. 4	Х		Х			

Ind. 5	Х					Х
Ind. 6						
Ind. 7	Х					Х
Ind. 8						
Ind. 9		Х		Х		
Ind. 10		Х	Х			
Ind. 11		Х				
Ind. 12						
Ind. 13		Х				
Ind. 14						
Ind. 15		Х		Х		
Ind. 16		Х	Х			
Ind. 17		Х				
Ind. 18		Х			Х	
Ind. 19				Х		Х
Ind. 20				Х	Х	Х
Ind. 21				Х	Х	
Ind. 22				Х	Х	Х
Ind. 23				Х		Х
Ind. 24					Х	
Ind. 25					Х	
Ind. 26					Х	
Ind. 27					Х	
Ind. 28					Х	
Ind. 29					Х	
Ind. 30						Х
Ind. 31						Х
Ind. 32						Х
Ind. 33						Х
Ind. 34						Х

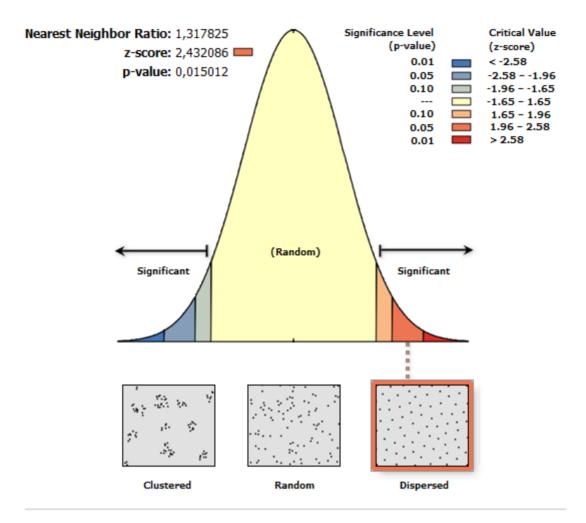
Table 4. Result of the Nearest Neighbor Analysis for male and female points

Average Nearest Neighbor Summary						
	Observed	Expected	Nearest	z-score	p-value	Study Area
	Mean	Mean	Neighbor			
	Distance	Distance	Ratio			
Male	3.38545	6.518314	0.519375	-7.298061	0.000000	10,707.080954
Female	13.875272	10.528918	1.317825	2.432086	0.015012	7,094.919399



Given the z-score of -7.30, there is a less than 1% likelihood that this clustered pattern could be the result of random chance.

Figure 2. Graphical result from the Nearest Neighbor Analysis for male *Osornophryne guacamayo*. Note that the dispersion pattern is "clustered".



Given the z-score of 2.43, there is a less than 5% likelihood that this dispersed pattern could be the result of random chance.

Figure 3. Graphical result for the Nearest Neighbor Analysis for female *Osornophryne guacamayo*. Note that the dispersion pattern is "dispersed".

Among the 36 toads marked for 3D mapping, only 9 male toads had enough recapture points to allow for the Kernel Density Analysis without further processing. These toads correspond to numbers 3 (Figure 4), 4 (Figure 5), 5 (Figure 6), 9 (Figure 7), 15 (Figure 8), 22

(Figure 9), 24 (Figure 10), 28 (Figure 11), and 30 (Figure 12). None of the adjacent toads showed overlap between them. Voxel size was counted as 8 for all 9 individuals processed.

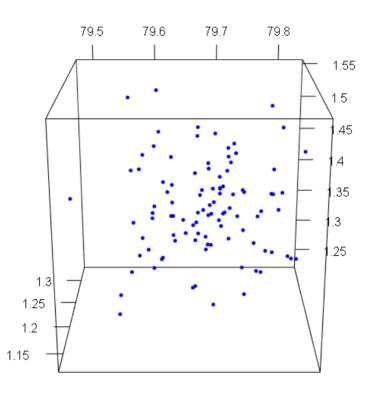
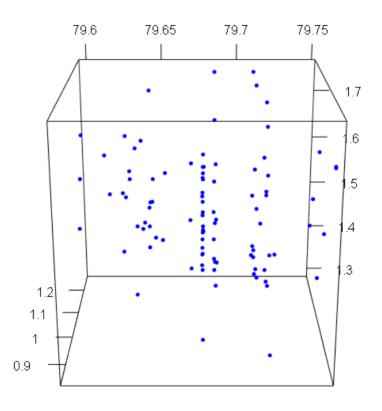


Figure 4. 3D plotting of 100 points for toad 3 where x=distance from start of transect, y=height, z=distance from the middle of the transect. All measurements are in meters.



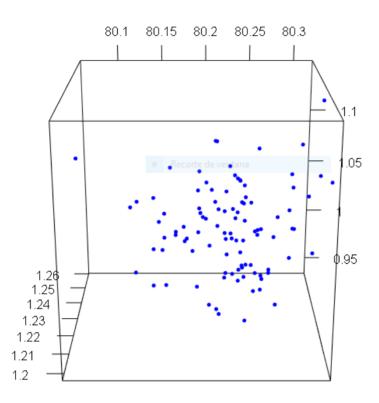


Figure 6. 3D plotting of 100 points for toad 5 where x=distance from start of transect, y=height, z=distance from the middle of the transect. All measurements are in meters.

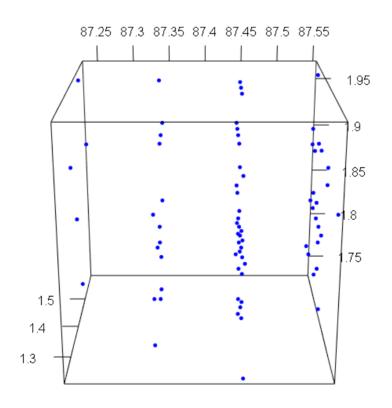


Figure 7. 3D plotting of 100 points for toad 9 where x=distance from start of transect, y=height, z=distance from the middle of the transect. All measurements are in meters.

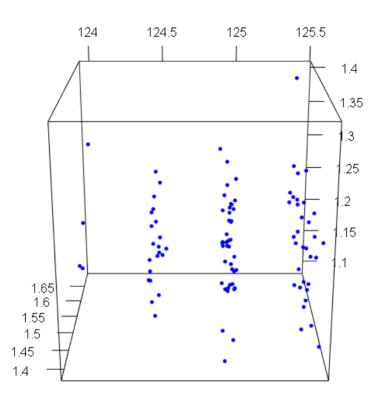
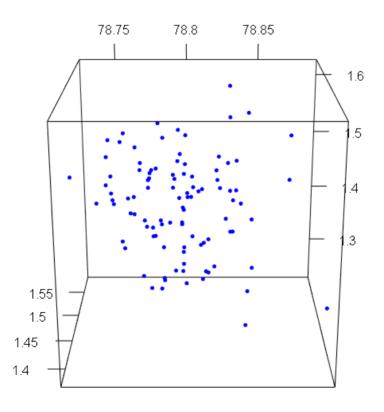


Figure 8. 3D plotting of 100 points for toad 15 where x=distance from start of transect, y=height, z=distance from the middle of the transect. All measurements are in meters.



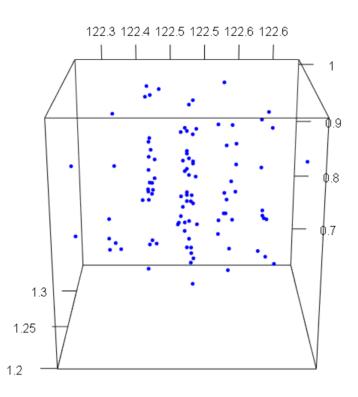
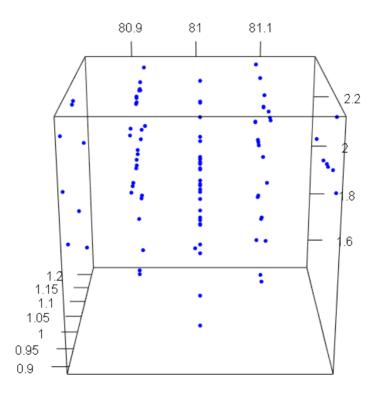


Figure 10. 3D plotting of 100 points for toad 24 where x=distance from start of transect, y=height, z=distance from the middle of the transect. All measurements are in meters.



24

Figure 11. 3D plotting of 100 points for toad 28 where x=distance from start of transect, y=height, z=distance from the middle of the transect. All measurements are in meters.

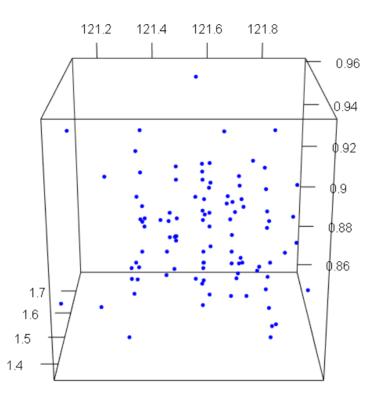


Figure 12. 3D plotting of 100 points for toad 30 where x=distance from start of transect, y=height, z=distance from the middle of the transect. All measurements are in meters.

DISCUSSION

The results of the Nearest Neighbor Analysis show a great difference regarding how males and females of O. guacamayo are arranged in their habitat, and their numbers. As it is the case with most species of amphibians, encounters with males greatly surpass the encounters with females. (de Souza, Kaefer, Lima, 2017, de Oliveira, Guimarães, Cabral, 2012, Ringler, Ursprung, Hödl, 2009, Lucas et al, 2008, Zina, Haddad, 2006, Toledo, Haddad, 2005). In certain studies, data shows that male of certain species can tolerate being relatively close (up to 1 mt apart) without agonistic interactions. (de Souza, Kaefer, Lima, 2017). Females of Osornophryne guacamayo did not show site fidelity (only 23.1% were recaptured). The reasons for this behavior could range from active movement throughout the night to lack of screening effort. Nonetheless, the hypothesis that better fits the observed data is that of a reproductive system similar to a lek for O. guacamayo. Some of the conditions of lek systems are not met, such as documented callings or a documented breeding season. (Toledo, Haddad, 2005). But others such as no signs of male parental care, females capable of moving to choose a wide variety of males, low operational sex ratios, and the inability of males to control essential resources for females support this system. (Toledo, Haddad, 2005). Because the study does not encompass all year activity, further research regarding seasonality and/or peaks of reproductive activity are highly encouraged.

Our study clearly suggests that males have a high site fidelity and the plausible existence of territories, even though no vocalization was documented. Very little movement was seen in males, most of them moved only centimeters. This is a behavior concordant with different species of anurans. (Zina, Haddad, 2006, Narvaes, Rodrigues, 2005). In some cases, an individual would stay still in one or two points for a whole night, deeming a KDE analysis impossible. Thus, the necessity of performing bootstraps. In this case, site fidelity could be equated to residency, but further annual research is needed. We note that home ranges could

be greater than reported because of the characteristics of the habitat. If toads moved deeper into the forest or climbed towards the canopy, they could not be followed. Thus, the detection of these toads would be almost impossible.

The lack of overlap among male home ranges strongly supports the notion of territoriality between males. Being the territory a defended place that does not permit the entrance of another males and mates being the resource to obtain. (Meuche, Linsenmair, Pröhl, 2012). De Oliveira, Guimarães, and Cabral (2012) define territoriality as moving less than 2 m from their first recorded position on successive sampling nights, a criterion that fit the data presented in the study. Hutter et al. (2013) follow a similar rule. Males do not show greater differences in the size of their home ranges, a characteristic that is shared among different species which tend to exploit the space in a relatively equal way. (Neu et al, 2016).

CONCLUSIONS

Dispersion rates differ greatly between males and females of *Osornoprhyne* guacamayo. Males show a clustered arrangement in their habitat and high site fidelity. On the other hand, females show a dispersed arrangement along their habitat and low site fidelity. Males occur much more frequently than females, thus, showing a low operational sex ratio. A lek-type of reproductive system is proposed to explain why males are so close and females are so dispersed. Study of male movement shows that home ranges are small and do not differ greatly between individuals. Lack of overlap between home ranges supports the possibly of territories happening within them.

Further research is necessary in order to know if females show home range behavior, how seasonality can affect the distribution of individuals among the habitat.

REFERENCES

- Cooper, N. W., Sherry, T. W., & Marra, P. P. (2014). Modeling three-dimensional space use and overlap in birds. *The Auk: Ornithological Advances*, 131(4), 681-693.
- De Oliveira, F. F. R., Nogueira, P. A. G., & Eterovick, P. C. (2012). Natural history of Phyllomedusa megacephala (Miranda-Ribeiro, 1926) (Anura: Hylidae) in southeastern Brazil, with descriptions of its breeding biology and male territorial behaviour. *Journal of natural history*, *46*(1-2), 117-129.
- Gluesenkamp, A. G. (1995). A new species of Osornophryne (Anura: Bufonidae) from Volcán Sumaco, Ecuador with notes on other members of the genus. *Herpetologica*, 268-279.
- Gluesenkamp, A. G., & Acosta, N. (2001). Sexual dimorphism in Osornophryne guacamayo with notes on natural history and reproduction in the species. *Journal of herpetology*, 35(1), 148-151.
- Guayasamin, J. M., & Funk, W. C. (2009). The amphibian community at Yanayacu Biological Station, Ecuador, with a comparison of vertical microhabitat use among Pristimantis species and the description of a new species of the Pristimantis myersi group. *Zootaxa*, 2220(2009), 41-66.
- Hoogmoed, M. S. (1987). New Osornophryne (Amphibia: Anura: Bufonidae) from the atlantic versant of the Andes in Ecuador. *Zoologische mededelingen*, *61*(16), 209-242.
- Hutter, C. R., Esobar-Lasso, S., Rojas-Morales, J. A., Gutiérrez-Cárdenas, P. D. A., Imba, H., & Guayasamin, J. M. (2013). The territoriality, vocalizations and aggressive interactions of the red-spotted glassfrog, Nymphargus grandisonae, Cochran and Goin, 1970 (Anura: Centrolenidae). *Journal of Natural History*, 47(47-48), 3011-3032.
- Lucas, E. M., Brasileiro, C. A., Oyamaguchi, H. M., & Martins, M. (2008). The reproductive ecology of Leptodactylus fuscus (Anura, Leptodactylidae): new data from natural temporary ponds in the Brazilian Cerrado and a review throughout its distribution. *Journal of Natural History*, 42(35-36), 2305-2320.
- Luger, M., Hödl, W., & Lötters, S. (2009). Site fidelity, home range behaviour and habitat utilization of male harlequin toads (Amphibia: Atelopus hoogmoedi) from Suriname: relevant aspects for conservation breeding. *Salamandra*, 45(4), 211-218.
- Meuche, I., Linsenmair, K. E., & Pröhl, H. (2012). Intrasexual competition, territoriality and acoustic communication in male strawberry poison frogs (Oophaga pumilio). *Behavioral Ecology and Sociobiology*, 66(4), 613-621.
- Mueses-Cisneros, J. J. (2003). EL GÉNERO OSORNOPHRYNE (AMPHIBIA: BUFONIDAE) EN COLOMBIA/The genus Osornophryne (Amphibia: Bufonidae) in Colombia. *Caldasia*, 419-427.

- Narvaes, P., & Rodrigues, M. T. (2005). Visual communication, reproductive behavior, and home range of Hylodes dactylocinus (Anura, Leptodactylidae). *Phyllomedusa: Journal of Herpetology*, 4(2), 147-158.
- Neu, C. P., Bisanz, S. S., Nothacker, J. A., Mayer, M., & Lötters, S. (2016). Male and female home range behavior in the Neotropical poison frog Ameerega trivittata (Anura, Dendrobatidae) over two consecutive years. *South american journal of herpetology*, *11*(3), 212-220.
- Ousterhout, B. H., & Burkhart, J. J. (2017). Moving beyond the plane: measuring 3D home ranges of juvenile salamanders with passive integrated transponder (PIT) tags. *Behavioral ecology and sociobiology*, *71*(4), 59.
- Páez-Moscoso, D. J., Guayasamin, J. M., & Yánez-Muñoz, M. (2011). A new species of Andean toad (Bufonidae, Osornophryne) discovered using molecular and morphological data, with a taxonomic key for the genus. *ZooKeys*, (108), 73.
- Páez-Moscoso, D. J., & Guayasamin, J. M. (2012). Species limits in the Andean toad genus Osornophryne (Bufonidae). *Molecular Phylogenetics and Evolution*, 65(3), 805-822.
- Pröhl, H. (2005). Territorial behavior in dendrobatid frogs. *Journal of Herpetology*, *39*(3), 354-366.
- R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
- Ringler, M., Ursprung, E., & Hödl, W. (2009). Site fidelity and patterns of short-and longterm movement in the brilliant-thighed poison frog Allobates femoralis (Aromobatidae). *Behavioral Ecology and Sociobiology*, 63(9), 1281-1293.
- Ron, S. R., Guayasamin, J. M., & Menendez-Guerrero, P. A. (2011). Biodiversity and Conservation Status of Amphibians of Ecuador En Heatwole, H., Barrio-Amorós, C. L., Wilkinson, J. W. (Eds.), *Amphibian Biology. Volume 9. Part 2* (pp. 129-186). Sydney, Australia: Surrey Beatty & Sons
- Sierra, R. Ed. (1999). Propuesta preliminar de un sistema de clasificación de vegetación para el Ecuador continental. Proyecto INEFAN/GEF-BIRF y EcoCiencia. Quito, Ecuador.
- Simpfendorfer, C. A., Olsen, E. M., Heupel, M. R., & Moland, E. (2012). Three-dimensional kernel utilization distributions improve estimates of space use in aquatic animals. *Canadian Journal of Fisheries and Aquatic Sciences*, 69(3), 565-572.
- Toledo, L. F., & Haddad, C. F. B. (2005). Reproductive biology of Scinax fuscomarginatus (Anura, Hylidae) in south-eastern Brazil. *Journal of Natural History*, *39*(32), 3029-3037.
- Tracey, J. A., Sheppard, J., Zhu, J., Wei, F., Swaisgood, R. R., Fisher, R. N. (2014). Movement-Based Estimation and Visualization of Space Use in 3D for Wildlife Ecology and Conservation. *PLoS ONE* 9(7): e101205. doi:10.1371/journal.pone.0101205

- Valenzuela-Sánchez, A., Harding, G., Cunningham, A. A., Chirgwin, C., & Soto-Azat, C. (2014). Home range and social analyses in a mouth brooding frog: testing the coexistence of paternal care and male territoriality. *Journal of Zoology*, 294(4), 215-223.
- Vivancos, A., Closs, G., & Tentelier, C. (2016). Are 2D space-use analyses adapted to animals living in 3D environments? A case study on a fish shoal. *Behavioral Ecology*, 28(2), 485-493.
- Werner, P., Elle, O., Schulte, L. M., & Lötters, S. (2010). Home range behaviour in male and female poison frogs in Amazonian Peru (Dendrobatidae: Ranitomeya reticulata). *Journal of Natural History*, 45(1-2), 15-27.
- Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70(1), 164-168.
- Zina, J., & Haddad, C. F. (2006). Ecology and reproductive biology of two species of Aplastodiscus (Anura: Hylidae) in the Atlantic forest, Brazil. *Journal of Natural History*, *40*(29-31), 1831-1840.